

# Larval development of the Mud Crab *Panopeus occidentalis* de Saussure, from Bermuda (Crustacea: Xanthoidea: Panopeidae)

R. W. Ingle

Department of Zoology, British Museum (Natural History), Cromwell Road, London SW7 5BD

## Introduction

Over 30 species of xanthid crabs have been reported from the waters of Bermuda (see Markham & McDermott, 1981: 1273) but the larval stages of only fourteen have been partly or completely described to date (see Table 1). Of the three *Panopeus* species, larval descriptions are available for *P. bermudensis* Benedict & Rathbun and *P. herbstii* H. Milne Edwards; the account of *P. occidentalis* is unpublished (Kurata, 1970) and may not be of this species but of *Hexapanopeus angustifrons* Benedict & Rathbun (see Martin *et al.*, 1984).

During a 1983 September–October visit to Bermuda the author collected an ovigerous specimen of *Panopeus occidentalis*. This was transported to the larval rearing laboratory in the British Museum (Natural History) and the larvae that hatched were reared to megalopal stage. The complete larval development of *P. occidentalis* is described from this material and the stages are compared with the account given by Costlow & Bookhout (1961*b*) of the larval development of *P. herbstii*.

Adults and juveniles of *P. occidentalis* are similar to those of *P. herbstii*. Rathbun (1930: 334) designated subspecies for both, but the subspecific status is now generally not recognised (Williams, 1965: 197, 198). Specimens of *Panopeus* collected on the shores of St George's Island, Bermuda, were provisionally identified on location by their distinctive colour patterns. Identifications were later confirmed using Rathbun (1930), Williams (1965) and from comparisons with specimens of *P. occidentalis* from Florida and *P. herbstii* from North Carolina in the BM(NH) Collections. The colour of Bermuda specimens of *P. occidentalis* varied from yellow-ochre to a mottled brown and with bands of brown on the walking legs, whereas *P. herbstii* had an overall greenish-brown colour with darker chelipeds and paler walking legs. One diagnostic feature of *P. herbstii* is the continuation of the dark colour, from the propodal prolongation of the chelipeds, onto the outer palmar surface; this feature was apparent only in the largest specimens collected. Verrill (1908: 353) reported *P. occidentalis* as 'not common in Bermuda'. During the present visit both species were found to be more or less equally represented on the mud flats at Ferry Reach, although the larger specimens of *P. occidentalis* and the small ovigerous female (18.0 mm c.l.) was collected from burrows on the lowest part of the shore during low tide.

## Material and Methods

The ovigerous female from which the larvae were reared was collected from a mud flat burrow on the lowest part of the shore exposed at low tide in the St David's Road region of Ferry Reach, Bermuda on 29 September 1983. Larvae were reared using methods and apparatus described by Rice & Ingle (1975: 104). Material was fixed in 5% formalin and later transferred to 70% IMS. Drawings and measurements were made with the aid of a *camera lucida* and using a Wild M20 microscope; details of setation were confirmed using interference contrast on an Olympus BH2 microscope. The material has been incorporated in the Collections of the British Museum (Natural History), accession number: 1984: 239, 240.

The eggs hatched on 5.10.1983 and the first megalops appeared on 14.11.1983; rearing was carried out at temperatures of 22–24°C.

Measurements: T.T. = distance between tips of dorsal and rostral spines; C.L. = carapace length from between the eyes to the postero-lateral margin.

## Descriptions

### *Panopeus occidentalis* de Saussure, 1857

non *Panopeus occidentalis*: Kurata, 1970 (= *Hexapanopeus angustifrons* Benedict & Rathbun)

#### FIRST ZOEAE

*Dimensions*: T.T. 1–1.1 mm, C.L. 0.4–0.5 mm.

*Carapace* (Fig. 1a): Dorsal spine evenly curved, stout proximally; rostral spine slightly curved, as long as dorsal spine; lateral spines short and stout; dorso-median elevation prominent; antero-median setules absent, a small pair of postero-median setules present (see inset to fig.); postero-lateral margin of carapace somewhat truncate and with very minute denticles (see inset).

*Eyes*: Partly fused to carapace.

*Antennule* (Fig. 1e): Unsegmented, with 3 terminal aesthetascs and one long seta.

*Antenna* (Fig. 1i): Spinous process long, with a small proximal dorsal spinule; distal half of process with many spines; exopod very small, narrowing distally, with 2 terminal setae (see inset).

*Mandible*: Incisor and molar processes differentiated.

*Maxillule* (Fig. 4a): Endopod 2-segmented, with 1,6 setae; basal endite with 5 spines/setae, coxal with 8 spines/setae.

*Maxilla* (Fig. 4e): Endopod 2-lobed, outer larger than inner slightly stepped and with 5 setae (3+2), inner lobe with 3 setae; basal endite 2-lobed, with 4+5 setae; coxal endite 2-lobed with 4+4 setae; scaphognathite with 3 long plumose setae and a stout plumose posterior projection.

*First maxilliped* (Fig. 4f): Basis with 10 setae arranged 2,2,3,3; endopod 5-segmented, 5th segment shorter than 4th, segments with 3,2,1,2,4+1 setae respectively; exopod incipiently 2-segmented, with 4 terminal plumose setae.

*Second maxilliped* (Fig. 4g): Basis with 4 setae; endopod 3-segmented, with 1,1,4+1 setae respectively; exopod incipiently 2-segmented, with 4 terminal plumose setae.

*Third maxilliped*: Not developed.

*Pereiopods*: Not developed.

*Abdomen* (Fig. 2a,3a): 5 segments + telson; 2nd segment with a pair of sub-acute, anteriorly directed, dorso-lateral processes; 3rd segment with a pair of small, acute, posteriorly directed, dorso-lateral processes; postero-lateral margins of 1st and 2nd segments rounded, 2nd with minute spinules (see inset, fig. 3a), 3rd–5th each extended into an acute process; postero-dorsal surface of 2nd–5th segments each with a small pair of setules near margin; posterior margins of segments 2–5 with very minute denticles (see inset, fig. 2a). Telson forks slightly diverging distally, each with one prominent dorsal spine and one small and one large lateral spine, forks minutely denticulate proximally (lower inset, fig. 2a); posterior margin of telson with 6 long setae.

#### SECOND ZOEAE

*Dimensions*: T.T. 1.4–1.5 mm, C.L. 0.6–0.7 mm.

*Carapace* (Fig. 1b): with 3 pairs of antero-median setules (see inset); postero-median setules longer than those of first zoea; postero-lateral margin of carapace with 1–2 setules (see inset); dorsal margin with pronounced elevation; submedian lobes of rostral base angular.

*Eyes*: Now free.

*Antennule* (Fig. 1f): With 4 aesthetascs and one seta.

*Antenna* (Fig. 1j): Spinous process with some long spines; proximal dorsal spinule very minute, absent in some specimens, exopod with only one terminal setule.

*Mandible*: unchanged.

*Maxillule* (Fig. 4b): Endopod setation unchanged; outer margin of basal endite with a plumose seta, distal margin with 8 spines/setae; setation of coxal endite unchanged.

*Maxilla* (Fig. 5c): Endopod, basal and coxal setation unchanged; scaphognathite with 10 long plumose setae.

*First maxilliped*: Setation of basis and of endopod unchanged; exopod with 6 terminal plumose setae.



**Fig. 1** *Panopeus occidentalis* de Saussure: a-d 1st-4th zoeae from lateral aspects; e-h antennule and i-l antenna of 1st-4th zoeae respectively; m right mandible of 4th zoea; scales = 0.1 mm.

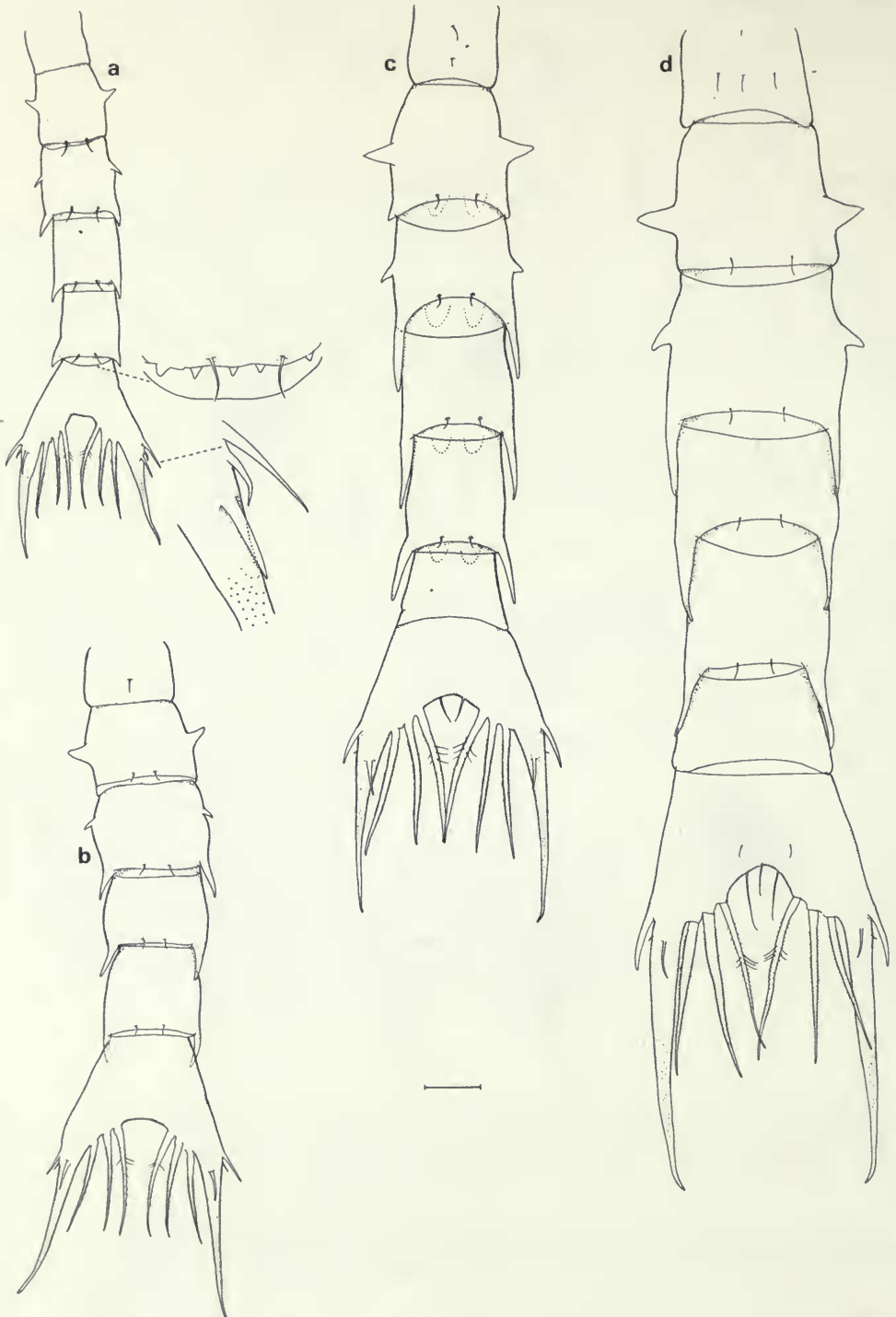
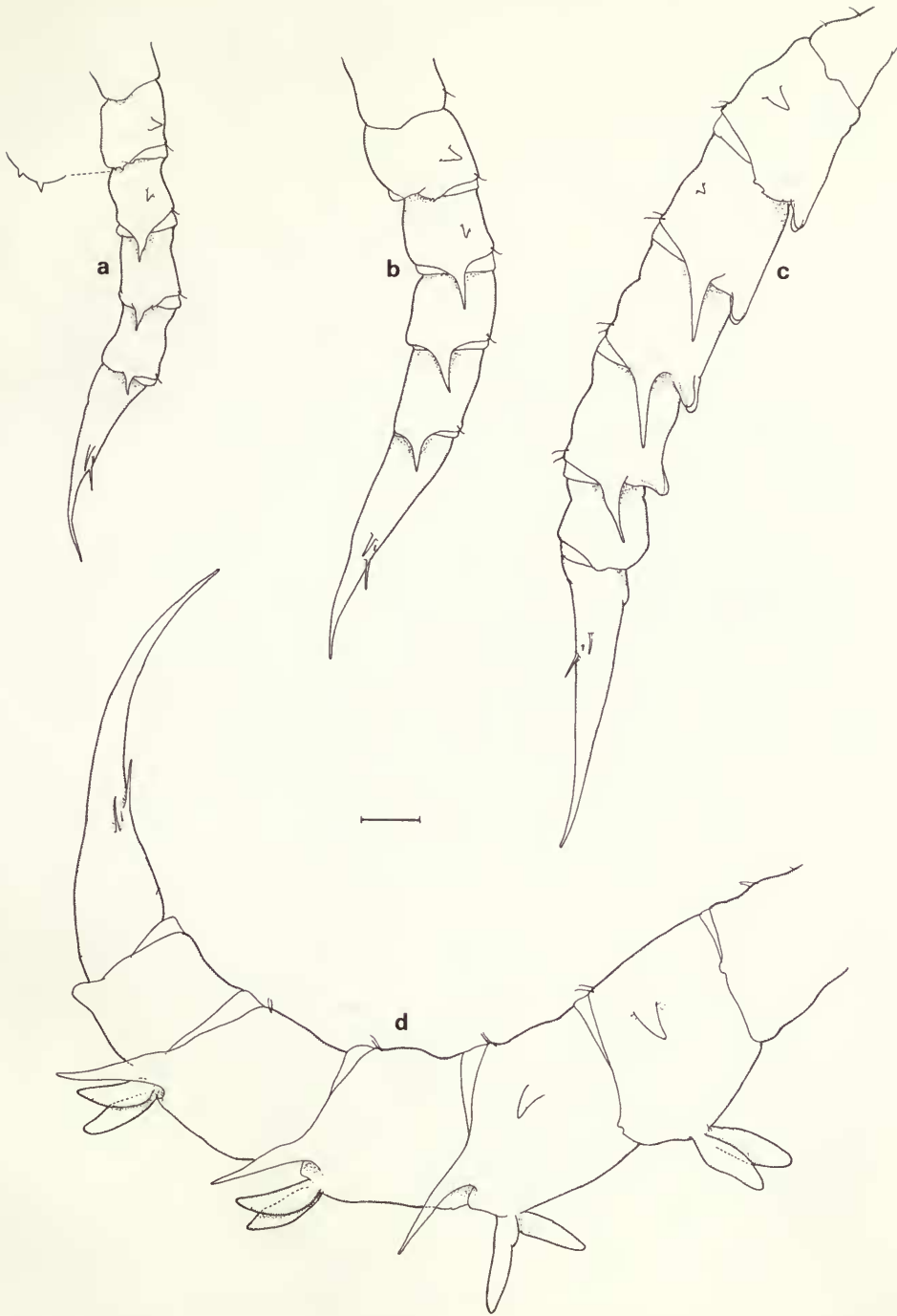


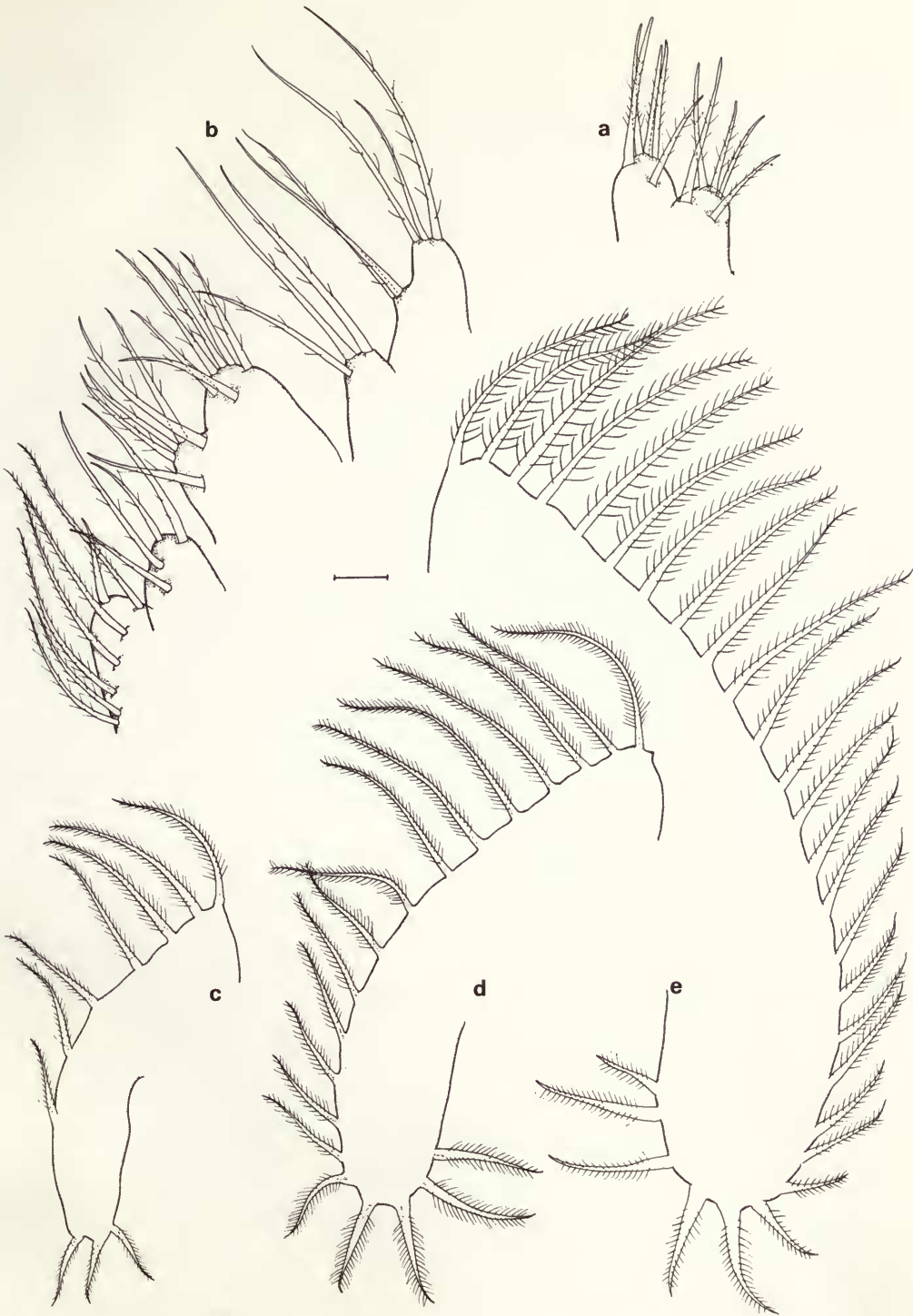
Fig. 2 *Panopeus occidentalis* de Saussure: abdomen and telson from dorsal aspects, a-d of 1st-4th zoeae respectively; scale = 0.1 mm.



**Fig. 3** *Panopeus occidentalis* de Saussure: abdomen and telson from lateral aspects, a-d of 1st-4th zoeae respectively: scale=0.1 mm.



**Fig. 4** *Panopeus occidentalis* de Saussure: maxillule a–d of 1st–4th zoeae respectively; e maxilla of 1st zoea, scale=0.02 mm; f, g 1st and 2nd maxilliped of 1st zoea; h 1st maxilliped endopod of 3rd zoea; scale=0.1 mm.



**Fig. 5** *Panopeus occidentalis* de Saussure: a maxilla basal endite of 3rd zoea; b maxilla distal endopod, basal and coxal endites of 4th zoeae; maxilla scaphognathite c-e of 2nd-4th zoeae respectively; scale = 0.02 mm.

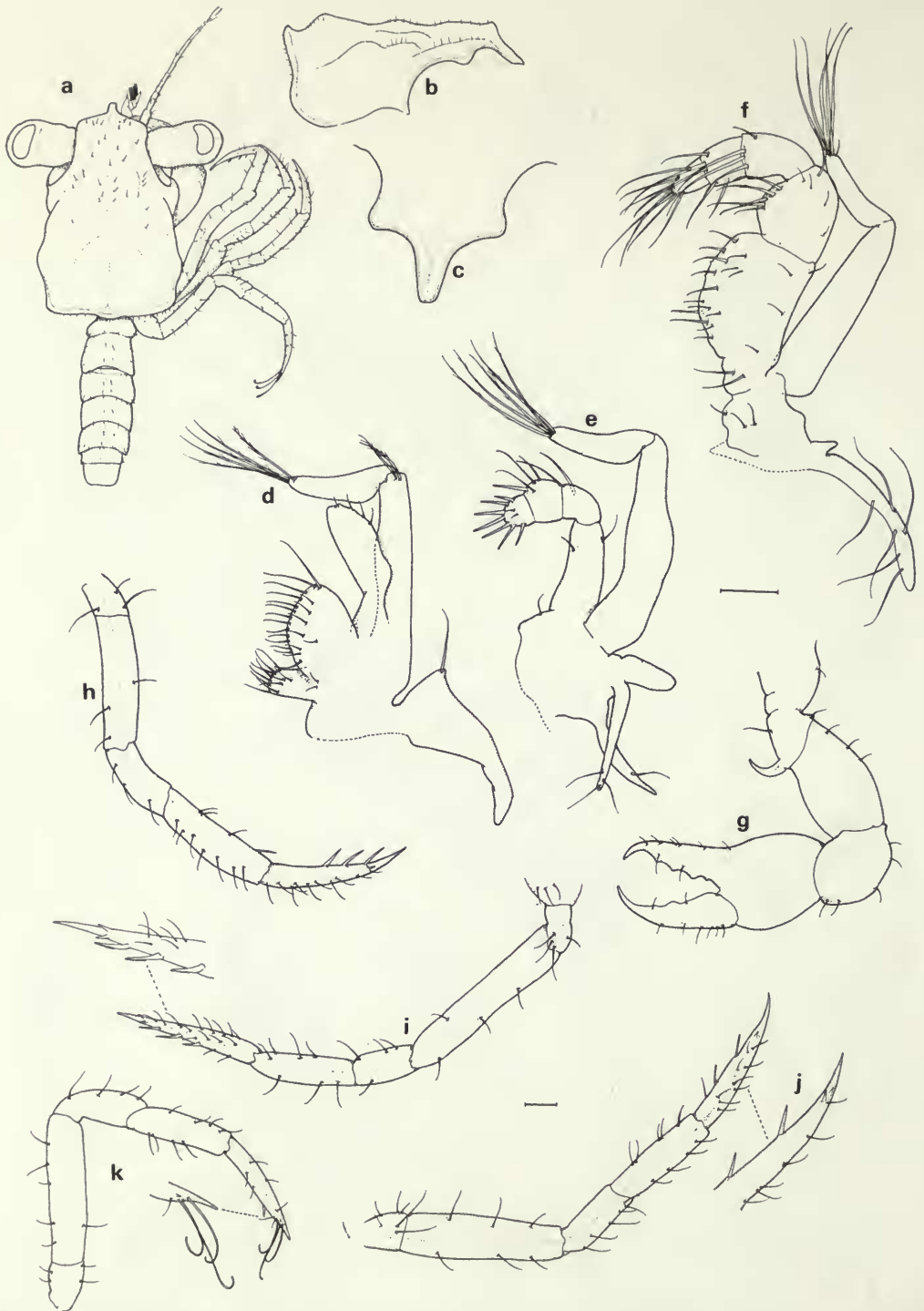


Fig. 6 *Panopeus occidentalis* de Saussure; megalopa—a from dorsal aspect; b carapace from lateral aspect; c rostrum from frontal aspect; d–f 1st–3rd maxillipeds respectively, scale=0.1 mm; g–k 1st–5th pereopods respectively, scale=0.1 mm.





**Fig. 7** *Panopeus occidentalis* de Saussure: megalopa—a maxillule; b basal and c coxal endites of maxilla; d maxilla; e basal and coxal endites of maxilla; f antennule; g antenna; h 1st pleopod; i right mandible; j telson and right uropod (ventral aspect); k abdomen from dorsal aspect; scales k to scale 1=0.1 mm. b,c,e to scale 2=0.02 mm; a,d,f,g to scale 3=0.1 mm; h,j to scale 5=0.1 mm; i to scale 4=0.05 mm.

*Second maxilliped*: Setation of basis and of endopod unchanged; exopod with 6 terminal plumose setae, an incipient 7th present in some specimens.

*Third maxilliped*: Not developed.

*Pereiopods*: Not developed.

*Abdomen* (Fig. 2b, 3b): Dorsal surface of 1st segment with a small setule; postero-lateral processes longer than those of first zoea.

### THIRD ZOEAE

*Dimensions*: T.T. 1.7–1.8 mm, C.L. 0.7–0.8 mm.

*Carapace* (Fig. 1c): Postero-lateral margin with 3–5 setules; dorsal margin with elevation more pronounced and the angular submedian lobes of rostral base more developed than those of second zoea.

*Antennule* (Fig. 1g): Now with an extra seta.

*Antenna* (Fig. 1k): Spinous process and exopod unchanged; endopod bud prominent, reaching for nearly  $\frac{1}{4}$  length of spinous process.

*Mandible*: Unchanged.

*Maxillule* (Fig. 4c): Setation of endopod unchanged; basal endite with 9 spines/setae; setation of coxal endite unchanged.

*Maxilla* (Fig. 5a,d): Setation of endopod unchanged; basal endite with 5+5 setae; coxal endite setation unchanged; scaphognathite with 19 plumose setae.

*First maxilliped* (Fig. 4h): Setation of basis unchanged; 5th segment of endopod almost as long as 4th and with 5+1 setae; exopod with 8 terminal plumose setae.

*Second maxilliped*: Setation of basis and of endopod unchanged; exopod with 8 (in some specimens 9) terminal plumose setae.

*Third maxilliped*: Now represented as a small bud.

*Pereiopods*: Present as unsegmented buds.

*Abdomen* (Figs 2c, 3c): with 6 segments + telson; postero-lateral processes longer than those of second zoea; 1st segment with 2 median setules on dorsal surface; segments 2–5 with incipient pleopod buds; innermost lateral spinule of telson forks very minute, posterior margin of telson with 8 setae.

### FOURTH ZOEAE

*Dimensions*: T.T. 2.3–2.4 mm, C.L. 0.9–1.0 mm.

*Carapace* (Fig. 1d): Dorsal spine with 2–3 small setules near base; angular submedian lobes of rostral base more developed than those of third zoea.

*Antennule* (Fig. 1h): With 9–10 aesthetascs and 1–2 setae.

*Antenna* (Fig. 1l): Endopod almost  $\frac{1}{2}$  length of spinous process.

*Mandible* (Fig. 1m): Mandibular palp represented as an unsegmented bud.

*Maxillule* (Fig. 4d): Setation on endopod unchanged; basal endite with 11 spines/setae; coxal endite with 9 setae.

*Maxilla* (Fig. 5b,e): Endopod setation unchanged; basal endite with 6+5 setae; coxal endite with 4+7 setae; scaphognathite with 27–28 plumose setae.

*First maxilliped*: Setation of basis and of endopod unchanged; exopod with 10 terminal plumose setae.

*Second maxilliped*: Setation of basis and of endopod unchanged; exopod with 10 (11 in some specimens) terminal plumose setae.

*Third maxilliped*: Represented as a larger bud than in the third zoea.

*Pereiopods*: First sub-chelate, 2nd–5th incipiently segmented.

*Abdomen* (Figs 2d, 3d): Segments 2–5 with well developed pleopod buds, 6th with postero-lateral margins obtusely produced; dorsal surface of 1st segment with 4 setules; dorsal surface of telson with 2 setules, posterior margin with 9 setae.

### MEGALOPA

*Dimensions*: C.L. 1.40 mm.

*Carapace* (Fig. 6a–c): Posteriorly slightly broadened, without tubercles, urogastric region elevated, a pair of indistinct carinae on orbital, protogastric, epibranchial and mesobranchial regions; hepatic regions slightly inflated; frontal region broad, with a narrow, truncate, medially concave rostrum directed obliquely downwards, submedian lobes rounded; dorsal surface and margins of carapace setose.

*Eyes*: Prominent, cornea slightly broader than peduncle.

*Antennule* (Fig. 7f): Peduncle 3-segmented, sparsely setose; exopod 4 segmented with a total of 14–15

aesthetascs, 4th segment long, thin and with one terminal and one subterminal seta, 1–2 small setae on segment 3; endopod 2-segmented, distal segment long, with 4 distal setae.

*Antenna* (Fig. 7g): Peduncle 3-segmented, with 2,2,2 setae respectively; flagellum 8-segmented, with 0,0,2,0,4,0,4,3 setae respectively.

*Mandible* (Fig. 7i): Mandibular palp 2-segmented, distal segment short and broad, with 10–11 setae.

*Maxillule* (Fig. 7a–c): Endopod reduced and unsegmented, with 3 proximal and 2 terminal setae; inner margin of basal endite with 3 setae, distal margin with a total of 17 spines/setae; coxal endite with 14–15 setae.

*Maxilla* (Fig. 7d,e): Endopod reduced to subcylindrical, terminally acute lobe with 1–2 long setae; basal endite with 9+6 setae; coxal endite with 6+9 setae; scaphognathite with 49–50 short plumose setae.

*First maxilliped* (Fig. 6d): Inner margin of coxal endite with 10–11 setae and with 1–2 proximal setae; inner margin and outer surface of basis with 21–22 setae; endopod with 4–5 short setae; exopod 2-segmented, proximal segment with 2 distal setae, distal segment with 5 long terminal setae; epipod well developed, with 1–2 setae.

*Second maxilliped* (Fig. 6e): Proximally almost devoid of setae; merus of endopod with 2 setae, carpus with 1–2, propodus with 4 setae and one spine, dactylus with 7 stout thin spines and 2 setae; exopod long, distal segment with 5 long terminal setae; 2 epipods bearing distal setae and one additional endite present.

*Third maxilliped* (Fig. 6f): Coxa and basis not differentiated, with 3–5 setae; margins and outer surface of endopod ischium with 18–22 setae distributed as shown, merus with 5–6 setae on inner upper surface, carpus with 4–5 setae, propodus with 5–6, dactylus with 7–8 setae; exopod 2-segmented, distal segment with 5 long and one shorter terminal setae; epipod long, with 6–7 setae.

*Cheliped* (Fig. 6g): Stout, moderately setose, ischium with a prominent curved spine; inner margin of propodal prolongation and of dactylus cut into obtuse and sub-acute teeth.

*Pereiopods 2–5* (Fig. 6h–k): Thin and setose, without ischial or basal spines; inner margin of dactylus of pereiopods 2–4 with 3,3,2 spines respectively; dactylus of 5th pereiopod with 3 long sub-distal setae, one small spine and a minute spinule.

*Abdomen & telson* (Fig. 7h–k): With 6-segments+telson and with numerous setae distributed as shown; postero-lateral margins of segments suboval; segment 6 short. Telson truncate, broader than long, posterior margin slightly concave, with 3 long plumose setae, 2 pairs of dorsal and one pair of ventral setae on telson surfaces. Exopods of 1st–4th pleopods with 15–16, 15, 16, 13–14 long plumose setae; exopods decreasing in length progressively from 1st–4th, that of 4th only slightly longer than peduncle; endopods with 2 or 3 coupling hooks on internal margin. Uropod without endopod, with 10 marginal setae on exopod distal segment, proximal segment with one seta.

## Remarks

A comparison of the present reared material of *Panopeus occidentalis* with the larval account of *P. herbstii* by Costlow & Bookhout (1961b) has revealed few differences between the zoeal stages of these two species but significant ones between the megalopas. These differences are summarised in Table 2. Details of setal patterns on the zoeal carapace, the first abdominal segment and telson, and on the abdominal segments of the megalopa of *P. herbstii* are not known. The submedian lobes of the carapace of *P. occidentalis* fourth zoea are not developed into the acute protrusions figured for this corresponding stage of *P. herbstii*. The megalopa of *P. occidentalis* is without the prominent 'rostral horns' figured for *P. herbstii* and in this respect it resembles the megalopa of *P. turgidus* (see Martin *et al.*, 1984, fig. 8(a)), a species placed by Abele (1970) into the genus *Eurypanopeus*. However, *P. turgidus* has long serrate spines on the posterior margin of the telson whereas *P. occidentalis* has relatively short plumose setae. It would appear that at least two types of megalopas are represented among closely related species assigned to the problematical genus *Panopeus* (viz. *P. herbstii*, *P. occidentalis* and *P. turgidus*). However, the zoeae of all three species can be clearly attributed to group I of the xanthid groups proposed by Martin (1984).

Larval stages are known for only 14 (see Table 1) of the 31 or more species of xanthid crabs reported from Bermuda waters (see Markham & McDermott, 1981). Published accounts of four of these, *Heteractaea ceratopus* (Stimpson), *Xantho denticulatus* (White), *Leptodius parvulus* Rathbun and *Eurytium limosum* (Say) are inadequate even for superficial comparative studies. The first zoea attributed to *Panopeus bermudensis* (Benedict & Rathbun) by Lebour (1944: 119,

**Table 1** Published accounts of larval and juvenile xanthoidean crabs reported from Bermudan waters.

<i>Carpilius corallinus</i> (Herbst)	Laughlin <i>et al.</i> 1983: 171–12, figs 1–11 (1st–5th zoeae).
<i>Eurypanopeus depressus</i> (Smith)	Birge 1883: 414, Pl. XXXI, fig. 12, Pl. XXXII, fig. 13 (2nd zoea); Hyman, 1925: 8–9, Pl. 1, figs 2,4,8,14,18, Pl. 2, figs 24,28,32, Pl. 9 (1st zoea); Costlow & Bookhout 1961a: 7–13, figs 1–41 (1st–4th zoeae, megal.); Martin <i>et al.</i> 1984: 562, 565, 574, 588, figs 10 <i>d</i> ,11 <i>d</i> , 13 <i>div</i> ,16,20, 23 <i>div</i> ,28,29,33 <i>div</i> ,40,41,42,46 (1st, 2nd, 3rd, 5th crab).
<i>Eurytium limosum</i> (Say)	Kurata <i>et al.</i> 1981: 19–25, figs 1–4 (1st–4th zoeae, megal. 1st crab); Andryszak & Gore 1981: 500–2 (zoeal & megal. features tabulated).
<i>Heteractaea ceratopus</i> (Stimpson)	Gurney 1936: 628, Pl. VII, figs 69–71 (1st zoea).
<i>Lobopilumnus agassizii</i> (Stimpson)	Lebour 1950: 377, fig. 7 D,E (1st zoea, as var. <i>bermudensis</i> ).
<i>Micropanope sculptipes</i> Stimpson	Andryszak & Gore 1981: 490–502, figs 1–6 (1st–4th zoeae, megal.).
<i>Panopeus bermudensis</i> Benedict & Rathbun	?Lebour 1944: 119, fig. 9 (1st zoea); Martin <i>et al.</i> 1984: 545–50, 556–7, 563–4, 566–9, 557–9, figs 2–5, 10a, 11a, 12, 13ai, 17, 21, 22, 23ai, 30, 31, 32, 33ai, 46, 47 (4th zoea, megal. 1st 2nd, 3rd, 5th crab).*
<i>Panopeus herbstii</i> H. Milne Edwards	Hyman, 1925: 9, Pl. 1, figs 5, 9, 15, 19, Pl. 2, figs 21, 25, 29, 33, Pl. 10, figs 116–124 (prezoea, 1st zoea); Costlow & Bookhout 1961b: 33–39, figs 1–6 (1st–4th zoeae, megal.); Andryszak & Gore 1981: 500–2 (zoeal & megal. features tabulated); Martin <i>et al.</i> 1984: 557–9, 564, 569, 579, figs 10b, 11b, 13bii, 14, 18, 23bii, 24, 25, 33bii, 34, 35, 36, 46, 47 (1st, 2nd, 3rd, 5th crab).
<i>Panopeus occidentalis</i> de Saussure	present account.
<i>Pilumnus dasyopodus</i> Kingsley	Sandifer 1974: 379–88, figs 1–6 (1st–4th zoeae, megal.); Bookhout & Costlow 1979: 2–13, figs 1–7 (1st–4th zoeae, megal); Andryszak & Gore 1981: 500–2 (zoeal & megal. features tabulated).
<i>Pilumnus sayi</i> Rathbun	McDonald & Lang 1976: 219 (abstract, no descript.); Bookhout & Costlow 1979: 13, fig. 7B (comp. with <i>P. dasyopodus</i> , megal. abd. pereopods figs); Andryszak & Gore 1981: 500–2 (zoeal & megal. features tabulated).
<i>Pseudomedeus agassizii</i> (A. Milne Edwards)	Costlow & Bookhout 1968: 205–211, figs 1–5 (1st–4th zoeae, megal. as <i>Leptodius agassizii</i> ); Andryszak & Gore 1981: 500–2 (zoeal & megal. features tabulated).
<i>Xantho denticulatus</i> (White)	Lebour 1944: 119, fig. 8 (1st zoea, as <i>Xanthodius denticulatus</i> ).
<i>Xanthodius americana</i> (de Saussure)	?Lebour 1944: 119, fig. 7 (1st zoea, as <i>Leptodius parvulus</i> ).

fig. 9) is almost certainly not this species (see Martin *et al.*, 1984: 541) and is assigned by Martin (1984) to his group II. Also questionable is the identification of the first stage zoea attributed by Lebour (1944: 119) to *Leptodius parvulus* (Fabricius) (see Wear, 1970: 86) and placed by Martin (1984) into group II; both of these above mentioned zoeae are 'piluminid types' (see Rice, 1980: 327). Lebour (1944) reported '*Leptodius parvulus*' as 'common in rocks and under stones between tide marks' but Verrill (1908: 340) noted it as 'a rare species at the Bermudas'. Markham & McDermott (1981: 1273) refer to this species as *Xanthodius americana* (de Saussure).

Martin (1984) has provided a useful key to the known xanthid zoeae of the American western Atlantic that will enable their identification to the groups he proposed and, in some instances, to species. In a more restricted context the combined features listed below may be adequate for distinguishing the zoeae of *Panopeus herbstii* and *P. occidentalis* from those of other species reported from Bermuda waters (see Table 1), except for *H. ceratopus* (that is insufficiently described) and

\*Martin, J. W., *et al.* 1985. *Journal of Crustacean Biology* 5 (1): 84–105 (1st–4th zoeae, megal.).

Table 2

	<i>P. herbstii</i>	<i>P. occidentalis</i>
FIRST ZOEAE		
Antennule		
aesthetascs:	3	3
setae	2	1
Antenna		
spinous process	distal $\frac{1}{4}$ spinulate	distal $\frac{1}{2}$ spinulate
proximal spinule on spinous process	?absent	present
terminal seta on exopod	1	2
Maxillule		
coxal endite	7 spines/setae	8 spines/setae
Maxilla		
scaphognathite	4 plumose setae + apical projection	3 plumose setae + apical projection
Carapace		
dorso-median elevation	?not prominent	prominent
SECOND ZOEAE		
Antennule		
aesthetascs	3	4
setae	2	1
Antenna		
spinous process	distal $\frac{1}{3}$ spinulate	distal $\frac{1}{2}$ spinulate
Maxillule		
coxal endite	7 spines/setae	8 spines/setae
THIRD ZOEAE		
Antennule		
endopod bud	developed	not developed
aesthetascs	3	4
Antenna		
spinous process	distal $\frac{1}{6}$ spinulate	distal $\frac{1}{2}$ spinulate
Maxillule		
coxal endite	7 spines/setae	8 spines/setae
Maxilla		
scaphognathite	18 plumose setae	19 plumose setae
FOURTH ZOEAE		
Antennule		
exopod	segmented	not segmented
Antenna		
spinous process	distal $\frac{1}{6}$ spinulate	distal $\frac{1}{2}$ spinulate
Maxillule		
basal endite	12 spines/setae	11 spines/setae
Maxilla		
basal endite	13 setae	11 setae
coxal endite	9 setae	11 setae
scaphognathite	25 plumose setae	27-28 plumose setae
MEGALOPA		
Carapace		
submedian lobes of frontal region	almost as broad as long	much longer than broad
produced into spines		obtuse
Antennule		
aesthetascs on exopod	18	14-15
exopod 4th segmt. subterminal setae	2	1

*continued overleaf*

Table 2—continued

	<i>P. herbstii</i>	<i>P. occidentalis</i>
endopod segments	1	2
disto-external margin 3rd ped. segment	with long setae	without setae
Antenna		
flagella segments	7	8
setation, ped. segments 1-3	2,1,1	2,2,2
Maxillule		
setation of endopod	7	5
basal endite	approx. 22 spines/setae	20 spines/setae
Maxilla		
endopod	not noticeably reduced, with many setae	reduced, with 1-2 setae
basal endite	18 setae (10+8)	15 setae (9+6)
coxal endite	14 setae	15 setae
First maxilliped		
setation of basis	18	21-22
endopod	terminally acute	spatulate
exopod	segments almost subequal	proximal segment longest
exopod distal segment	6 terminal setae	5 terminal setae
proximal segment	1 outer distal seta	2 outer distal setae
Second maxilliped		
endopod, propodus	?without a disto-external spine & with 6 setae	with a disto-external spine & with 4 setae
dactylus	13 spines/setae	7 spines & 2 setae
Third maxilliped		
inner margin of ischium	10 setae	13-14 setae
Pleopods		
setation of exopods 1-4	15,15,15,12	15-16,15,16,13-14
setation of uropod exopod	8	10
Telson		
posterior margin	with 2 long setae/spines and 3 short setae	with 3 short plumose setae

the first zoea of *E. limosum* (from which it cannot be separated at present). 1. Carapace lateral spines present (absent in *P. bermudensis* Benedict & Rathbun). 2. Dorso-lateral processes present only on 2nd and 3rd segments of abdomen (on 2nd-5th segments in '*P. bermudensis* Lebour'). 3. Antennal exopod small (as long as spinous process in *P. sayi*, *P. dasypodus*, *X. americana* and *L. agassizii*; half as long in *C. corallinus*). 4. Postero-lateral processes of abdomen short in first zoea and submedian lobes of rostral base not developed as 'pre-orbital spines' from second zoea onwards (postero-lateral processes long in first zoea and a pair of long 'pre-orbital' spines present from second zoea onwards in *P. agassizii*). 5. Each telson fork with 2 lateral spines, one sometimes minute (only one lateral spine present in all stages of *M. sculptipes* and *E. depressus* and from second stage onwards in *E. limosum*). 6. Spinous process of antenna spinulate (?smooth in *X. denticulatus*). The megalopa of *P. occidentalis* is without 'rostral horns' (i.e. protrusions of the submedian lobes), a feature which readily distinguishes it from the megalopas of other Bermuda xanthids known at present except for *P. dasypodus* and *P. sayi* from which it is separated by having only a prominent curved ischial spine on the first pair of pereopods and no ischial or coxal spines on the second to fifth pairs.

### Acknowledgements

The visit to the Bermuda Biological Station was partly sponsored by an Exxon Corporation Fellowship. I wish to thank Dr Wolfgang Sterrer, Director of the Biological Station and his staff for providing the facilities for holding ovigerous crabs and for their assistance with various matters during my visit. Dr A. L. Rice kindly read the manuscript.

### References

- Abele, L. G. 1970. *The marine decapod Crustacea of the northeastern Gulf of Mexico*. Masters Thesis, Florida State University, Tallahassee, Florida (not seen).
- Andryszak, B. L. & Gore, R. H. 1981. The complete larval development in the laboratory of *Micropanope sculptipes* (Crustacea, Decapoda, Xanthidae) with a comparison of larval characters in western Atlantic xanthid genera. *Fishery Bulletin of the U.S. Fish and Wildlife Service*. Washington D.C. **79**: 487–506.
- Birge, E. A. 1883. Notes on the development of *Panopaeus sayi* (Smith). *Studies from the Biological Laboratory, Johns Hopkins University*. Baltimore. **2** (4): 411–426.
- Bookhout, C. G. & Costlow, J. D. 1979. Larval development of *Pilumnus dasypodus* and *Pilumnus sayi* reared in the laboratory (Decapoda Brachyura, Xanthidae). *Crustaceana. International Journal of Crustacean Research*. Leiden. Supplement **5**: 1–16.
- Costlow, J. D. & Bookhout, C. G. 1961a. The larval development of *Eurypanopeus depressus* (Smith) under laboratory conditions. *Crustaceana. International Journal of Crustacean Research*. Leiden. **2**: 6–15.
- 1961b. The larval stages of *Panopeus herbstii* Milne-Edwards reared in the laboratory. *Journal of the Elisha Mitchell Scientific Society*. Chapel Hill, N.C. **77**: 33–42.
- 1968. Larval development of the crab, *Leptodius agassizii* A. Milne Edwards in the laboratory (Brachyura, Xanthidae). *Crustaceana. International Journal of Crustacean Research*. Leiden. Supplement **2**: 203–213.
- Gurney, R. 1936. Notes on some Decapod Crustacea of Bermuda—III–V. *Proceedings of the Zoological Society of London* **3**: 619–630.
- Hyman, O. W. 1925. Studies on the larvae of crabs of the family Xanthidae. *Proceedings of the United States National Museum*. Washington, D.C. **67**: 1–22.
- Kurata, H. 1970. Studies on the life histories of decapod Crustacea of Georgia: Part III. Larvae of decapod Crustacea of Georgia. *Unpublished report*. University of Georgia Marine Institute. Sapelo Island (not seen).
- , Heard, R. W. & Martin, J. W. 1981. Larval development under laboratory conditions of the xanthid mud crab *Eurytium limosum* (Say, 1818) (Brachyura: Xanthidae) from Georgia. *Gulf Research Reports*. Gulf Coast Research Laboratory, Ocean Springs, Mississippi **7**: 19–25.
- Laughlin, R. A., Rodriguez, P. J. & Marval, J. A. 1983. Zoal stages of the coral crab *Carpilius corallinus* (Herbst) (Decapoda, Xanthidae) reared in the laboratory. *Crustaceana. International Journal of Crustacean Research* **44**: 169–186.
- Lebour, M. V. 1944. II. Larval crabs from Bermuda. *Zoologica*, New York **29**: 113–128.
- 1950. Notes on some larval decapods (Crustacea) from Bermuda. *Proceedings of the Zoological Society of London* **120**: 369–379.
- Markham, J. C. & McDermott, J. J. 1981. A tabulation of the Crustacea Decapoda of Bermuda. *Proceedings of the Biological Society of Washington* **93**: 1266–1276.
- Martin, J. W. 1984. Notes and bibliography on the larvae of xanthid crabs, with a key to the known xanthid zoeas of the Western Atlantic and Gulf of Mexico. *Bulletin of Marine Science*, Coral Gables **34**: 220–239.
- , Felder, D. L. & Truesdale, F. M. 1984. A comparative study of morphology and ontogeny in juvenile stages of four western Atlantic xanthid crabs (Crustacea: Decapoda: Brachyura). *Philosophical Transactions of the Royal Society of London B* **303**: 537–604.
- McDonald, H. J. & Lang, W. 1976. The larval development of *Pilumnus sayi* Rathbun reared in the laboratory. *American Zoologist*. Utica, N.Y. **16**: 219.
- Rathbun, M. J. 1930. The cancroid crabs of America of the families Euryalidae, Portunidae, Atelecyclidae, Cancridae and Xanthidae. *Bulletin of the United States National Museum*. Washington D.C. **1523**: i–xvi, 1–610.
- Rice, A. L. 1980. Crab zoeal morphology and its bearing on the classification of the Brachyura. *Transactions of the Zoological Society of London* **35**: 271–424.
- & Ingle, R. W. 1975. The larval development of *Carcinus maenas* (L.) and *C. mediterraneus* Czerniavsky (Crustacea, Brachyura, Portunidae) reared in the laboratory. *Bulletin of the British Museum (Natural History) Zoological Series*. London **28**: 101–119.

- Sandifer, P. A.** 1974. Larval stages of the crab, *Pilumnus dasypodus* Kingsley (Crustacea, Brachyura, Xanthidae), obtained in the laboratory. *Bulletin of Marine Science*. Coral Gables. **24**: 378-391.
- Saussure, H. de** 1857. Diagnosis de quelques Crustacés nouveaux de l'Amerique tropicale. *Revue et Magasin de Zoologie Pure et Appliquée*. Paris **9**: 501-505.
- Verrill, A. E.** 1908. Decapod Crustacea of Bermuda; 1-Brachyura and Anomura. Their distribution, variations, and habits. *Transactions of the Connecticut Academy of Arts and Sciences*. New Haven **13**: 299-474.
- Wear, R. G.** 1970. Notes and bibliography on the larvae of xanthid crabs. *Pacific Science*, Honolulu **24**: 84-89.
- Williams, A. B.** 1965. Marine Decapod Crustaceans of the Carolinas. *Fishery Bulletin of the U.S. Fish and Wildlife Service*. Washington, D.C. **65**: i-xi, 1-298.

Manuscript accepted for publication 12 December 1984

#### **Addendum**

Recently, Williams, A. B. 1983. Fishery Bulletin of the National Oceanic and Atmospheric Administration, Washington, D. C. 81 4: 868-872 (published October 1984) assigned bermudan material of *P. herbstii* to *P. lacustris* Desbonne, 1867